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2012

Ryberg, P., Taylor, E., and Taylor, T. 2012 The First Permineralized Microsporophyll of the Glossopteridales: Eretmonia macloughlinii sp. nov. International Journal of Plant Sciences, 173(7): 812-822.

Published version: http://dx.doi.org/10.1086/666667

Int. J. Plant Sci. 173(7):812–822. 2012.

1058-5893/2012/17307-0007$15.00 DOI: 10.1086/666667

THE FIRST PERMINERALIZED MICROSPOROPHYLL OF THE GLOSSOPTERIDALES: *ERETMONIA MACLOUGHLINII* SP. NOV.

Patricia E. Ryberg,[1,*] Edith L. Taylor,* and Thomas N. Taylor*

*Department of Ecology and Evolutionary Biology and Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, U.S.A.

Eretmonia du Toit is a microsporophyll genus attributed to the Permian Glossopteridales. Microsporophylls are scale leaves (smaller leaves with morphology similar to that of *Glossopteris* leaves) that bear clusters of sporangia at the end of stalks attached to the petiole of the sporophyll. Late Permian permineralized specimens of *Eretmonia* from the central Transantarctic Mountains in Antarctica reveal the first anatomical information of the genus. Numerous veins run the length of the petiole and alternate with large canals/air spaces; the veins and canals are separated by increasing amounts of parenchyma. The ground tissue of the leaves is composed of isodiametric parenchyma of varying diameters. Beneath the epidermis is a hypodermis two to three layers thick. Pollen sac walls are a single layer thick with a tapered apex and bulbous base. The simplicity of the bisaccate pollen grains does not suggest a specialized form of pollination but rather that the glossopterids were wind pollinated.

Keywords: glossopterids, Permian, Antarctica, pollen, microsporophyll, *Eretmonia*.

Introduction

The Glossopteridales are a group of extinct seed plants that dominated the Southern Hemisphere during the Permian (300–252 Ma). Glossopterid fossils dominate Permian terrestrial deposits to such an extent that Permian floras of Gondwana are also known as *Glossopteris* floras. The glossopterids consist of numerous genera representing disarticulated parts of the plant—that is, *Glossopteris* (Brongniart 1828) leaves, *Vertebraria* (Royle 1833 ex McCoy 1847) roots, *Araucarioxylon* (Kraus 1870) wood (but see Philippe [1993, 2011] on the usage of this name), and various genera of reproductive organs. Many of the reproductive structures are associated with the glossopterids by their presence in the same matrix rather than by organic attachment (e.g., *Rigbya* Lacey et al. 1975, *Arberia* White 1908, and the majority of megasporangiate structures). The leaves assigned to *Glossopteris* are widespread in Gondwana, common, and morphologically very similar; thus, they provide little information as to true glossopterid diversity. Some whole-plant reconstructions have been suggested for the Glossopteridales (Retallack and Dilcher 1988; Pigg and Nishida 2006), but no definitive evidence—either attachment or consistent association—is available for a reconstruction of the complete plant, including the reproductive structures. Until individual organs within the glossopterids can be found in organic attachment to each other, the true affinities and diversity cannot be determined.

Research on glossopterid reproductive structures has focused on megasporophylls, resulting in the erection of numerous genera (Adendorff 2005; Ryberg 2009; McLoughlin 2011). Little work has been done on glossopterid permineralized pollen structures, most likely because impression material indicates such a conservative morphology that all pollen organs have been placed in only a few genera. If pollen sacs are found dispersed in the matrix, they are given the name *Arberiella* (Pant 1958); if attached to a scale leaf, they are placed in *Eretmonia* (du Toit 1932), *Squamella* (White 1978), *Glossotheca* (Surange and Maheshwari 1970), or *Nesowalesia* (Pant 1977), on the basis of the shape of the scale leaf. Genera initially thought to be glossopterid microsporophylls include *Kendostrobus* (Surange and Chandra 1972), which has whorls of microsporangia attached helically to an axis, and *Gondwanolepsis* (Banerjee 1984), *Ghoshialepsis* (Banerjee 1984), and *Mahudaea* (Banerjee 1984), which are all scale leaves with glossopterid-like venation. In *Kendostrobus*, the presence of monolete spores and the arrangement of the sporangia on the axis suggest affiliation with a plant clade other than the Glossopteridales. The scale leaves described by Banerjee (1984) do not definitively have sporangia attached and may just be vegetative leaves and therefore not microsporophylls. The only publications to date that have presented information on permineralized pollen structures are those of Gould and Delevoryas (1977) and Nishida et al. (2002) from the Bowen Basin of Australia; Schopf (1970) from the Transantarctic Mountains, East Antarctica; and Lindström et al. (1997) and Holdgate et al. (2005) from the Prince Charles Mountains, East Antarctica. The presence of *Protohaploxypinus* pollen grains in the pollen chamber of ovules and in pollen sacs unites the megasporophylls and microsporophylls of the Glossopteridales (Taylor and Taylor 1987; Ryberg 2010). In this study, new anatomically preserved fossils that can be assigned to *Eretmonia* are described from permineralized Antarctic peat, and these specimens are compared with impressions from

[1] Author for correspondence; e-mail: rybergp@ku.edu.

Manuscript received January 2012; revised manuscript received February 2012.

across Gondwana to illustrate the conservative nature of microsporangiate structures of the glossopterids.

Material and Methods

Blocks of silicified peat with anatomically preserved plants come from the Skaar Ridge locality (lat. 84°48.718′S, long. 163°18.193′E) in the central Transantarctic Mountains, at the head of the Beardmore Glacier. The locality on Skaar Ridge is part of the upper Buckley Formation (Barrett and Elliot 1973; Barrett et al. 1986), and the peat has been dated as Late Permian on the basis of palynomorphs (Farabee et al. 1991; for additional information, see Ryberg 2010). Specimens were collected during the 2010–2011 Antarctic field season.

Antarctic fossils were sectioned and peeled using the acetate peel technique (Galtier and Phillips 1999) with 50% hydrofluoric acid, and peels were mounted on microscope slides with Eukitt (Kindler, Freiburg, Germany). Fossils were imaged with a Leica 5000C digital camera using a compound microscope. Images were processed using Adobe Photoshop CS3. Antarctic specimens, slides, and images are housed in the University of Kansas Natural History Museum, Division of Paleobotany, collection (KUPB) under specimen numbers 16809 and 16897 and slide numbers 24303–24342 and 26601–26609.

Geological setting. The Upper Permian strata of the Beardmore Glacier region have been reconstructed as a braided river system (Isbell 1991). The Skaar Ridge deposits are believed to be organic material accumulated in a backswamp formed by an abandoned river channel. Volcanic activity at the head of the foreland basin of the Transantarctic Mountains provided a source of silica for silicification (Collinson 1991). The silicified peat is bracketed by fluvial sandstones, based on the presence of mixed chert-sandstone blocks (Taylor and Taylor 1987).

Results

Class—Glossopteridopsida Banerjee 1984

Order—Glossopteridales Banerjee 1984

Family—Eretmoniaceae Maheshwari 1990

Genus—Eretmonia *du Toit 1932 emend. Lacey et al. 1975*

Type Species—Eretmonia natalensis *du Toit 1932*

Eretmonia macloughlinii *Ryberg, E. Taylor et T. Taylor sp. nov.*

Specific diagnosis. Helically arranged laminar microsporophylls with a long, thick petiole; anastomosing veins run the length of sporophyll and alternate with large canals. Two small vascularized stalks adnate to the midrib region; each produces a cluster of pollen sacs. Pollen sacs attached to stalk in spirals or whorls. Microsporangia, each with acute apex and bulbous base, walls a single cell layer, and cells elongate and loosely spiraled from apex to base. Pollen bisaccate, taeniate, of the *Protohaploxypinus* type.

Holotype. 16897B figures 1–6, designated here.

Type locality. Skaar Ridge, Beardmore Glacier region, central Transantarctic Mountains, Antarctica.

Type unit/formation. Upper Buckley Formation.

Age. Late Permian.

Etymology. The specific epithet is in honor of Dr. Stephen McLoughlin, one of the foremost paleobotanists in the study of the Glossopteridales.

Description

General features. Two specimens were available for study. One (16897) shows numerous sporophylls and pollen sacs in cross section and paradermal section, distal to the apex of the axis to which they were attached (fig. 1). The second (16809) consists of two clusters of pollen sacs.

Microsporophylls. The arrangement of the sporophylls indicates that they were helically attached to an axis (fig. 1). The presence of microsporangia on the adaxial side of the outermost sporophylls suggests that sporangia were attached to the adaxial surface of a sporophyll (fig. 1). Two to four vascular bundles enter the sporophyll (fig. 2*A*), are separated by a canal or air space (herein referred to as canals), and increase in number through dichotomies along the length of the petiole (fig. 2*C*). No distinctive midrib is present in the sporophyll. The petiole is thick (2 mm) and narrow (9.4 mm)

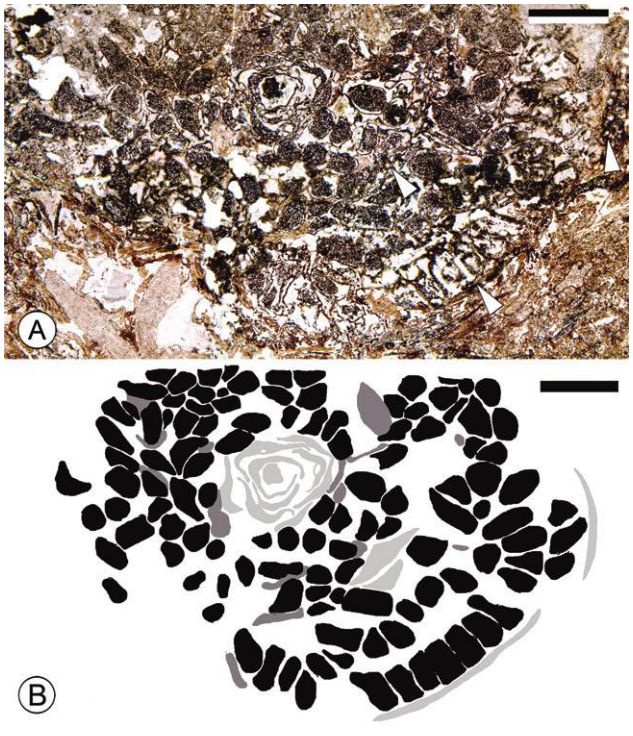

Fig. 1 *Eretmonia macloughlinii* Ryberg, E. Taylor et T. Taylor sp. nov. *A*, Cross section of holotype (KUPB 16897B) showing apical spiral of scale leaves surrounded by pollen sacs and affiliated sporophylls (arrowheads). KUPB slide 24320, scale bar = 2 mm. *B*, Line drawing of *A*. Black = pollen sacs, light gray = microsporophylls, dark gray = stalks and branchlets, scale bar = 2 mm.

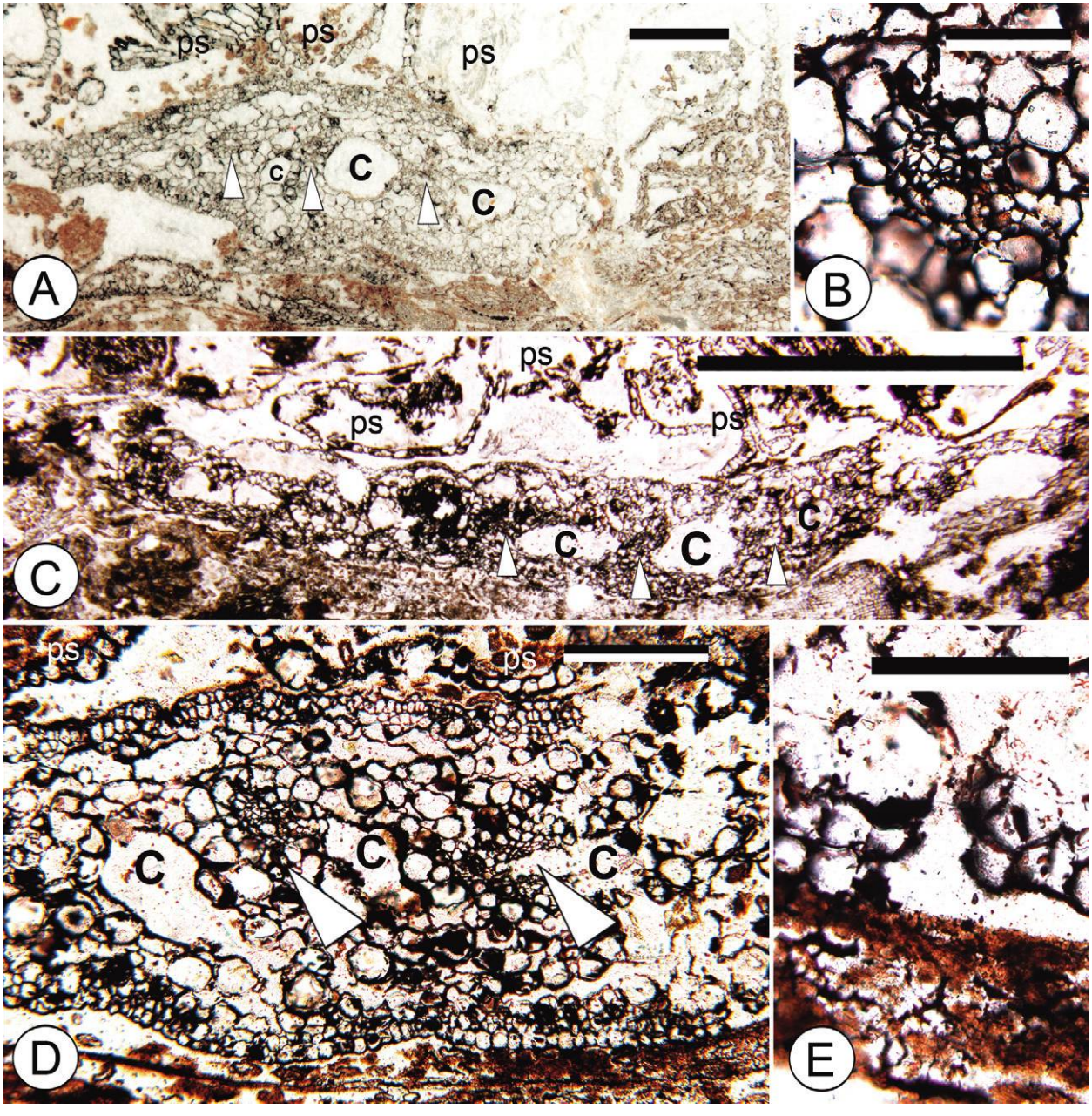

Fig. 2 *Eretmonia macloughlinii* Ryberg, E. Taylor et T. Taylor sp. nov. *A*, Oblique cross section of the microsporophyll petiole base showing vascular bundles (arrowheads) and intervening canals or air spaces (C); pollen sacs (ps) are at the top of the image. KUPB 16897B side peel 39, scale bar = 0.5 mm. *B*, Oblique cross section of a vascular bundle in the sporophyll with an abaxial phloem lacuna. KUPB slide 24324, scale bar = 0.1 mm. *C*, Oblique cross section of the lamina of the microsporophyll. Arrowheads = vascular bundles, C = canals or air spaces, ps = pollen sacs. KUPB slide 24334, scale bar = 2 mm. *D*, Oblique cross section of microsporophyll petiole showing vascular bundles (arrowheads) alternating with canals (C) and upper and lower epidermis with hypodermis. The vascular bundle on the left is magnified in *B*. ps = pollen sacs. KUPB slide 24324, scale bar = 0.25 mm. *E*, Oblique cross section of stoma on the abaxial surface of microsporophyll, higher magnification from lower right of *D*. KUPB slide 24324, scale bar = 0.1 mm.

and expands into a thin (1–1.2 mm thick) and wide (26.3 mm) lamina. The ground tissue of the microsporophyll consists of isodiametric parenchyma (0.1–0.2 mm in diameter; fig. 2*D*) with a line of medially located vascular bundles alternating with large canals (fig. 2*C*). The ground tissue is not differentiated into palisade and spongy mesophyll. Vascular bundles consist of tracheids with scalariform thickenings and a lacuna where the phloem was located (fig. 2*B*). Small cells surround the xylem and phloem lacuna, indicating the presence of a bundle sheath. Canals run the entire length of the lamina, do not contain an epithelial lining, and measure 0.4–1.6 mm in diameter (fig. 2*C*, 2*D*). Directly beneath the adaxial epidermis

is a hypodermis two to three cells thick; beneath the abaxial epidermis, the hypodermis is one to two cells thick (fig. 2*D*). Stomata are sunken on the adaxial and abaxial surfaces (fig. 2*E*). Anastomosing venation generates narrow and elongate meshes, and epidermal cells are cuboidal (40–90 μm) with dark contents in the center (fig. 4*B*, black arrow).

In a cross section of the microsporophylls within the bud, a large space, forming a bulge on the adaxial surface of the sporophyll, can be seen medially on the petiole (figs. 3*B*–3*E*, 4*A*). In this case, the stalks that bear the pollen sacs are not preserved, and this space represents their vasculature. Basally on the sporophyll a single large space occurs (fig. 3*D*, 3*E*); moving distally, this space divides in two (fig. 3*B*, 3*C*) and shortly is no longer present in the lamina (fig. 3*A*), suggesting that the stalks have extended above the sporophyll to produce pollen sacs. In specimens where tissue of the stalk is preserved, closer to the midrib the stalks have a larger diameter, indicating that they are attached at the midrib rather than the lateral lamina. Extending out from the midrib, the stalks get progressively smaller (fig. 5, black arrow). Each stalk contains a single vascular bundle with tracheids containing helical thickenings (fig. 4*D*).

Pollen sacs. The stalks that arise from the petiole produce a tight spiral of pollen sacs (figs. 2, 4*B*). The main stalk of each cluster of sporangia gives off vascularized branchlets with alternately to spirally attached sporangia (figs. 4*B*, 5*A*, white arrows). Each microsporangium is attached by its apex to these branchlets (fig. 4*B*, 4*C*). Sacs have a constricted apex made up of a single layer of cells forming a short neck (fig. 4*E*). The cells loosely spiral outward from the apex and increase in number, giving the surface an anastomosing appearance and the pollen sac a bulbous base (fig. 4*F*). The surface of a pollen sac appears ridged, with the periclinal walls forming the ridges and the abutting walls between two cells creating the furrows (fig. 4*F*). No distinctive region for pollen release is evident in the microsporangia. The contents of all the pollen sacs are mature pollen grains with no gametophyte tissue remaining, indicating that all pollen sacs were mature at the time of preservation.

Pollen. Pollen grains have a smooth external surface and endoreticulations beneath the saccus surface (fig. 6*A*–6*C*). The corpus is globose, and it bears taeniae (striations) across the cappus (fig. 6*B*) and sacci that are attached laterally in a subequatorial position (fig. 6*A*). This pollen appears most similar to the *sporae dispersae* taxon *Protohaploxypinus*.

Glossopteris schopfii *leaves*. Microsporophylls were preserved in leaf mats of *Glossopteris*. The mesarch xylem with prominent lacunae surrounded by a bundle sheath are identifying characteristics of the glossopterid leaf *G. schopfii* Pigg (fig. 6*D*).

Discussion

Affinities of Microsporophylls

The current literature on *Eretmonia* does not mention whether sporangia are attached to the adaxial or abaxial surface of the sporophyll (Surange and Maheshwari 1970; Surange and Chandra 1975; McLoughlin 2011). Du Toit (1932) mentioned the presence of sporangia on the adaxial surface of the sporophyll, but preservation of the genus as impressions/compressions has prevented the determination of pollen sac attachment to the sporophyll. In this study, the presence of sporangia inside the outermost sporophylls may be evidence that the microsporangia are attached to the adaxial surface of at least the outermost sporophylls.

Two species of *Glossopteris* leaves have been described from the permineralized peat at the Skaar Ridge locality (Pigg 1990). *Glossopteris skaarensis* has a distinctive midrib region in the leaves, broad polygonal meshes formed by the vasculature, and epidermal cells with a sinuous margin (Pigg 1990). The large canal in the microsporophyll could be considered analogous to the midrib region of *G. skaarensis*, but the diameter of the canals of *Eretmonia macloughlinii* (0.4–1.6 mm) is much greater than that of the vascular bundles of *G. skaarensis* (0.2–0.5 mm). In addition, there is an adaxial bulge formed by the adnate stalks, which produce pollen sacs in *E. macloughlinii* rather than the abaxial bulge of the midrib in *G. skaarensis*. Furthermore, the presence of vascular bundles between the canals in *E. macloughlinii* indicates that they were not lacunae where vasculature may have been. The abrupt decrease in thickness of the lamina of *G. skaarensis* once lateral of the midrib is absent in *E. macloughlinii*, where there is a gradual tapering of the lamina to the distal margins. The epidermal cells of *E. macloughlinii* are cuboidal, whereas the epidermal cells of *G. skaarensis* are rectangular with sinuous margins (45 μm wide $\times$ 24 μm high; Pigg 1990).

The second species of *Glossopteris* leaf from Skaar Ridge is *G. schopfii*, identified by the presence of phloem lacunae, a bundle sheath around the vascular bundles, anastomosing vascular bundles forming narrow elongate meshes, and epidermal cells with straight margins (Pigg 1990). *Eretmonia macloughlinii* has many of the features observed in *G. schopfii*, such as the narrow elongate meshes and epidermal cells with straight margins (fig. 4*B*). The most distinctive feature of *G. schopfii*—the presence of phloem lacunae—is inconsistent in *E. macloughlinii*, as some vascular bundles do not have lacunae, whereas others in the same section have abaxial lacuna similar to *G. schopfii* (fig. 2*B*). In addition, even some vascular bundles have a central or adaxial lacuna. The wide range of lacunae in the microsporophyll may be a result of preservation and does not definitively place the microsporangiate structure with *G. schopfii*. The bundle sheath in *E. macloughlinii* is not as prominent as in *G. schopfii*, but smaller-diameter parenchyma cells immediately surround the xylem and become progressively larger the farther they are located from the vasculature (fig. 2*D*). The size of the vascular bundles is also significantly smaller than in vegetative *Glossopteris* leaves.

The apical buds of both *G. skaarensis* and *G. schopfii* have been described from Skaar Ridge (Pigg and Taylor 1993). The bud of *G. skaarensis* contains leaves identical to the isolated leaves in the matrix, with a prominent midrib lacuna and a thin lamina on either side of the midrib. These features are not observed in the bud of *E. macloughlinii*, providing further support for the notion that the pollen structure is not affiliated with *G. skaarensis*. The bud of *G. schopfii* is similar to that of *E. macloughlinii*, with overlapping leaves (scale leaves in *E. macloughlinii*) enclosing the apex of the axis. There is a slight bulge in the adaxial region of the midrib of

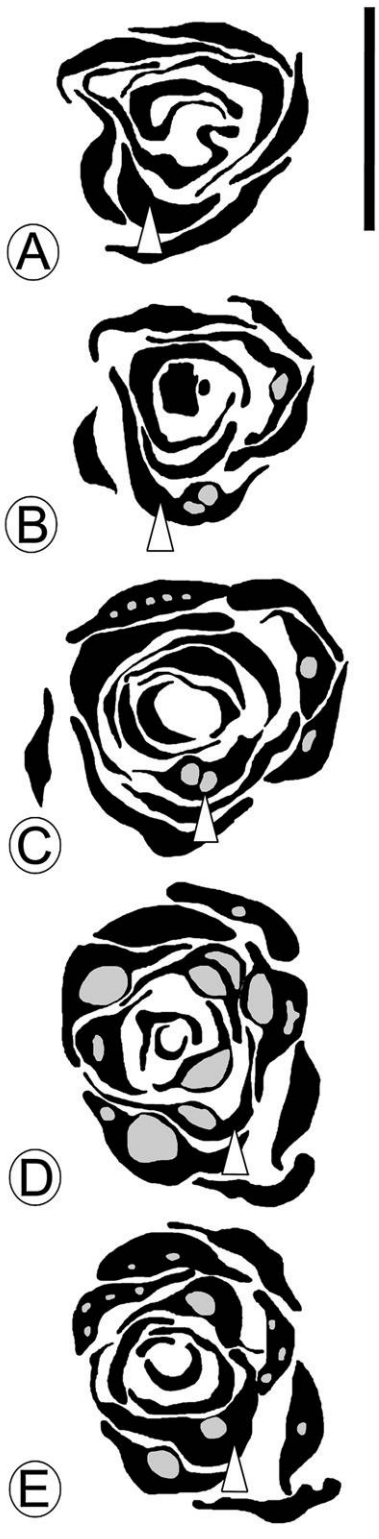

Fig. 3 Line drawings of cross sections of sporophylls near the apex of the pollen structure. Arrowheads point to the same sporophyll throughout sections. Black = sporophyll, gray = canals, scale bar = 2 mm. *A*, Distalmost section of sporophylls. 16897B side peel 25. *B*, More proximal section showing a few canals present in the sporophylls. The sporophyll at the arrowhead has two canals where the adnate stalks were located. KUPB slide 24324. *C*, Medial section of sporophylls. Note the sporophyll at the arrowhead showing two canals for the adnate stalks. KUPB slide 24329. *D*, More proximal section of sporophylls. Note that the canal at the arrowhead is a single large canal at this level and not two canals as in more distal sections. KUPB 16897B side peel 50. *E*, Most proximal section of sporophylls with only a small canal present. KUPB slide 24334.

G. schopfii, where the vascular bundles of the midrib are located. In both *E. macloughlinii* and *G. schopfii* leaves within the bud, lacunae are present lateral to the midrib, and these span the width of the lamina. In *G. schopfii*, these are the location of vascular bundles (fig. 18 of Pigg and Taylor 1993). Because of incomplete preservation in *E. macloughlinii*, however, we cannot determine whether these are the location of vascular bundles or represent the canals that run the length of the sporophyll (fig. 1*A*).

The presence of large canals or air spaces in *E. macloughlinii* is unique. No species of glossopterid leaf or megasporophyll has been described with large canals alternating with vascular bundles running the length of the sporophyll. The condition of the material prevents the determination of whether the canals were produced schizogenously or lysigenously. Several hypotheses could be proposed as to the purpose of these canals—for example, the prevention of herbivory of the pollen—but without more anatomical detail, the function of these canals cannot be determined. The distinctive canals may be specialized for the microsporophylls and never observed in vegetative leaves or megasporophylls, or they may function similarly to the air spaces seen in the root *Vertebraria* (Decombeix et al. 2009). The evidence presented on the anatomical features of *E. macloughlinii* unites the microsporophylls with the hypothesized "*Glossopteris schopfii*" plant. Lending support to this assignment is the presence of *G. schopfii* leaf mats surrounding all of the pollen sacs (fig. 6*D*) and the complete absence of *G. skaarensis* in the same peat specimens.

Glossopterid Microsporangia

Arber (1905) first described microsporangia from Permian deposits in New South Wales, Australia, but could not conclusively determine that sporangia on the surface of the sporophyll were glossopterid, since the glossopterids had been defined as pteridophytes. He compared the fossils to microsporophylls of the Cycadales but focused heavily on comparisons to fern groups with the understanding that *Glossopteris* was a fern. No spores or pollen were found in his specimens that would have allowed assignment to either the pteridophytes or the seed plants. *Eretmonia* was formally described from the Upper Permian Beaufort Group in Kwazulu-Natal province in South Africa as a scale leaf with glossopterid venation and two depressions containing sporangia (du Toit 1932).

Eretmonia and glossopterid pollen sacs characterized under the name *Arberiella* have been found across Gondwana, but studies have focused on gross morphological features and the pollen contained within the sporangia rather than on anatomical and surface features because of the state of preservation (mostly impressions and a few compressions; Pant and Bhatnagar 1973; Lacey et al. 1975; Chandra and Surange

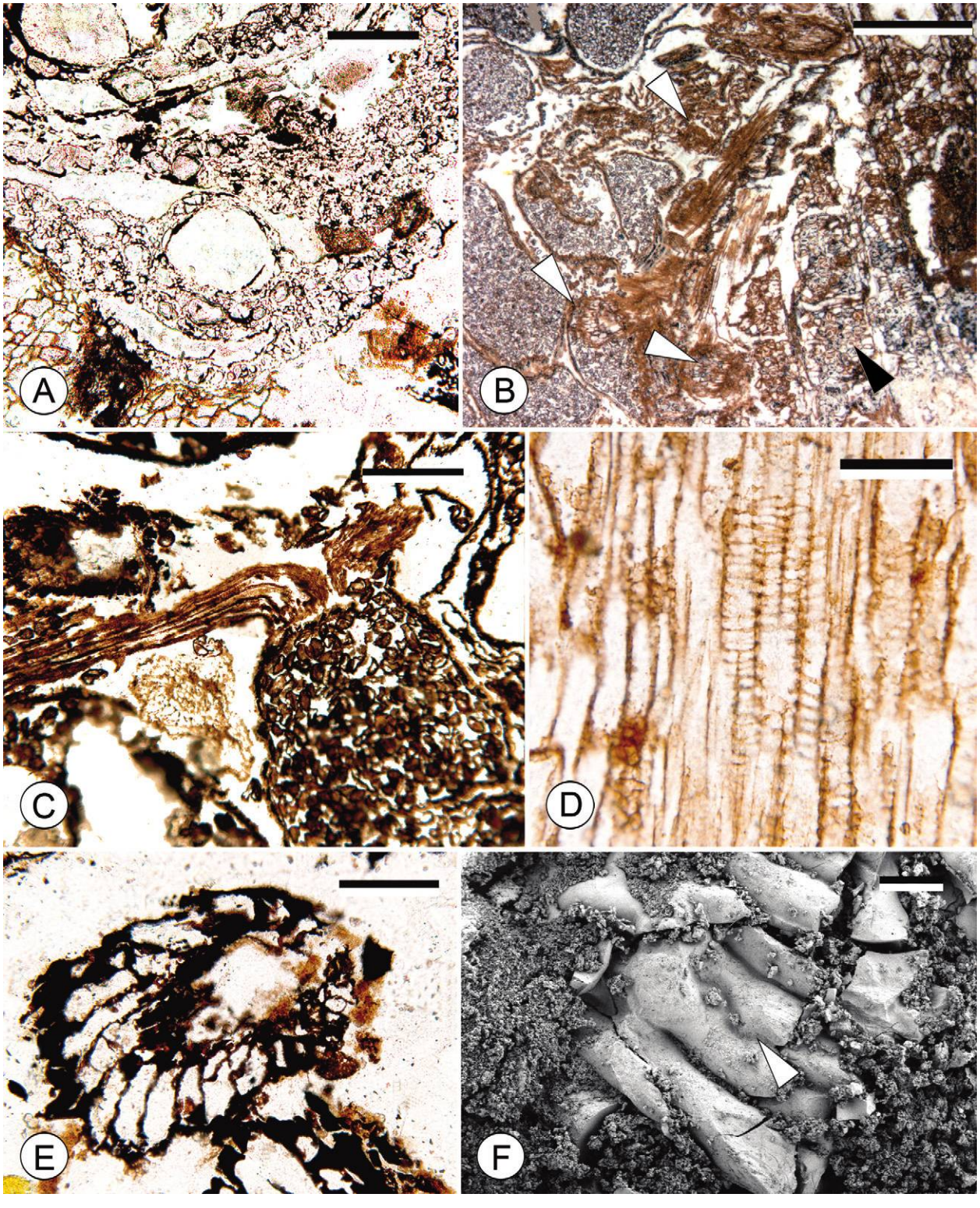

Fig. 4 *Eretmonia macloughlinii* Ryberg, E. Taylor et T. Taylor sp. nov. *A*, Oblique cross section of a microsporophyll. The large space on the adaxial surface is the position of the adnate pollen sac stalks. KUPB slide 24335, scale bar = 0.25 mm. *B*, Section of pollen sacs and paradermal section of sporophyll showing pollen sacs attached to branchlet (white arrowheads). Cuboidal epidermal cells of sporophyll are at the lower right (black arrowhead). KUPB slide 26603, scale bar = 1 mm. *C*, Oblique section of a pollen sac showing basal attachment to a branchlet. KUPB slide 24324, scale bar = 0.25 mm. *D*, Oblique longitudinal section of stalk vasculature showing helical tracheid thickenings. KUPB slide 26604, scale bar = 0.1 mm. *E*, Oblique cross section near the apex of a pollen sac showing the single cell layer that forms the surface of the sporangium. The cell arrangement here shows the beginning of the spiral toward the base of the sporangium. KUPB slide 24324, scale bar = 0.1 mm. *F*, SEM of pollen sac wall illustrating ridges formed by sporangial wall cells and furrows formed by the abutting walls of the individual cells. The arrowhead points to a possible division furrow between two cells. Scale bar = 30 μm.

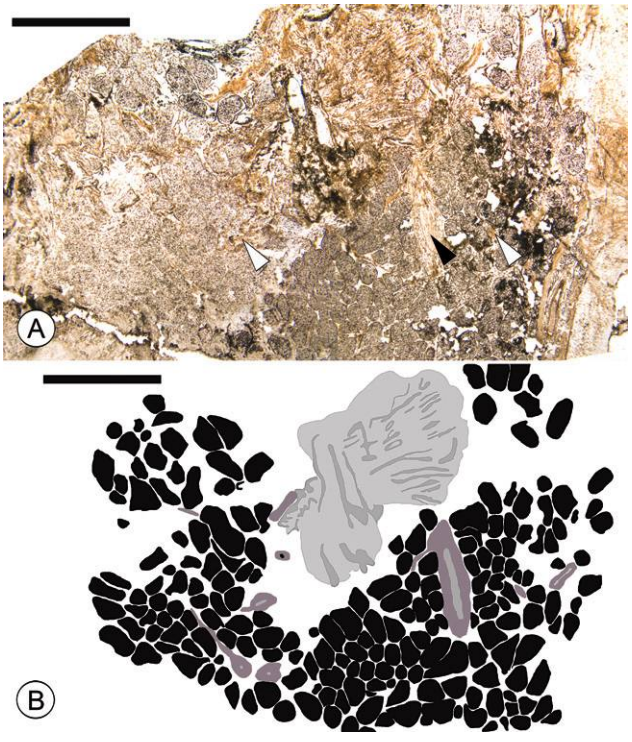

Fig. 5 *Eretmonia macloughlinii* Ryberg, E. Taylor et T. Taylor sp. nov. *A*, Oblique paradermal section of sporophyll and cross section of two clusters of pollen sacs. Darker pollen sacs on the right represent one cluster, and lighter pollen sacs on the left represent the second. Sporophyll lamina is located between the two (*center*, *top*). The black arrowhead points to stalk, and the white arrowheads point to branchlets. KUPB slide 26604, scale bar = 2 mm. *B*, Line drawing of *A* to delimit different tissues of *Eretmonia*. Black = pollen sacs, dark gray = stalks and branchlets, medium gray = vasculature, light gray = laminar tissue, scale bar = 2 mm.

1977; Rigby et al. 1988; Zavada 1991; Lindström et al. 1997; Ryberg 2009).

Previously described permineralized glossopterid pollen sacs from the Bowen Basin of Australia were assigned to *Arberiella*; they consisted of sporangial walls a single cell layer thick and contained bisaccate pollen (Gould and Delevoryas 1977). A preliminary report on additional fossils from this locality suggested that the sporophylls were spirally arranged on an axis (Nishida et al. 2002). Permineralized *Arberiella* from the Prince Charles Mountains in Antarctica are classified as *Arberiella* sp. cf. *A. africana* (Lindström et al. 1997). The sporangial walls of *A. africana* and *E. macloughlinii* are nearly identical, but the sporophyll is absent in the Prince Charles Mountains fossils, which distinguishes them from the Skaar Ridge specimens. Future studies may show that the sporophyll associated with *A. africana* is identical to *E. macloughlinii*, which would confirm the conservative nature of the microsporophyll morphology as identified from impression specimens (Surange and Chandra 1972; Holmes 1974; Anderson and Anderson 1985; Rigby et al. 1988; Holmes 1995; Ryberg 2009).

The majority of pteridosperm microsporangiate structures from the Paleozoic and Mesozoic consist of branching systems with the sporangia attached to the abaxial surface of a leaflike microsporophyll (e.g., Lyginopteridales, Callistophytales, and Corystospermales) or to terminal branchlets (e.g., Caytoniales; Taylor et al. 2009). The genus *Nesowalesia* is similar to the Paleozoic pteridosperms, with its cup-shaped sporophyll containing sporangia on the concave surface (Pant 1977). *Nesowalesia*, from the Upper Permian Illawarra Coal Measures of Australia and the Upper Permian deposits in Orissa, India, is unlike other glossopterid microsporophylls and is associated with the glossopterids on the basis of the presence of *Arberiella*-type pollen sacs, even though the attachment of the sporangia is unlike that in other glossopterid genera (Pant 1977; Rigby and Chandra 1990). *Nesowalesia* has not been found in attachment to other plant organs, and its orientation and organization within the whole plant is unknown.

The other three genera of glossopterid microsporophylls are all characterized by a leaflike sporophyll with pairs of stalks bearing clusters of sporangia. These include *Eretmonia*, a genus found throughout Gondwana; *Glossotheca*, from the Upper Permian of Orissa and Bihar, India (Surange and Maheshwari 1970); and *Squamella*, from the Upper Permian Illawarra Coal Measures in New South Wales, Australia (White 1978). The major difference among these three genera is the number of pairs of stalks attached to the sporophyll—that is, one pair in *Eretmonia*, two or more pairs in *Glossotheca*, and an unknown number in *Squamella*. The microsporophyll is often referred to as a scale leaf, as it is smaller than a *Glossopteris* leaf and is considered to be analogous to the fertile scales found in gymnosperms in bearing a cluster or clusters of sporangia on one side of the scale. *Squamella* has been reconstructed with scale leaves arranged helically around a central axis forming a pollen cone (White 1978, figs. 20, 21; Melville 1983). White's (1978) diagnosis for the genus *Squamella* is uninformative, as "reproductive structure genus of *Glossopteris*" does not indicate exactly what features distinguish the genus. Diagnoses of the species provide the morphology of the genus as spirally arranged scale leaves with sporangial clusters. It should be noted that several authors have questioned the hypothesized reconstruction of *Squamella* since its first publication, suggesting that the attached scale leaves may be a vegetative bud given that sporangia are not seen attached in the helically arranged leaves (Melville 1983; Pigg and Taylor 1993). The two clusters of sporangia on each microsporophyll of these Antarctic specimens link them to *Eretmonia*. The helical arrangement of microsporophylls in *E. macloughlinii* confirms that microsporophylls of the glossopterids are organized into a reproductive region on the plant and are probably a cone.

The conservative nature of the morphology of *Eretmonia* microsporophylls from contemporaneous deposits across Gondwana suggests that this type of microsporangium evolved early in the life history of the glossopterids. Dehiscence of pollen has been observed along the longitudinal striations and could probably occur between any two cells (Lindström et al. 1997). The single layer of cells constituting the wall of the pollen sac, the lack of vasculature extending into the sporangia, and the presence of mature pollen indicate that all sporangia are mature and at the point of dehiscence at time of fossilization. There does not appear to be a specialized cell layer, such as an annulus, for dehiscence to occur in a particular portion of the sporangium.

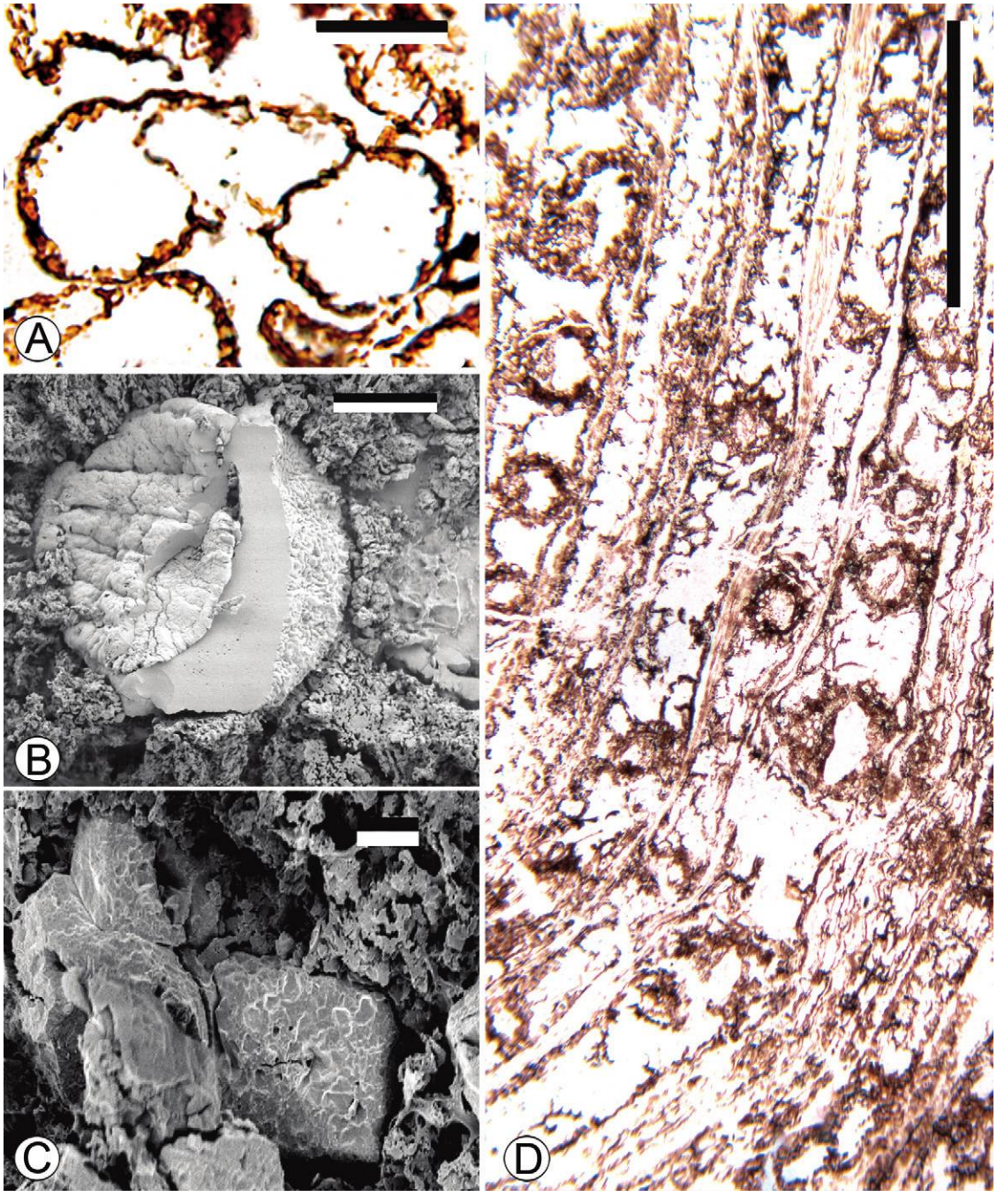

Fig. 6 *Eretmonia macloughlinii* Ryberg, E. Taylor et T. Taylor sp. nov. *A*, Equatorial section through a single pollen grain of the *Protohaploxypinus* type under transmitted light with two large sacci surrounding the central corpus and endoreticulations faintly visible along the inner margins of the sacci. KUPB slide 24321, scale bar = 25 μm. *B*, SEM of a single pollen grain in oblique view showing taeniae on the surface of the corpus (*left*) and endoreticulations on the inner saccus wall (*right*). Scale bar = 10 μm. *C*, SEM of sacci with surface view of endoreticulations. Scale bar = 2 μm. *D*, Cross section of *Glossopteris schopfii* leaves that surround the microsporophylls in the matrix. KUPB slide 24305, scale bar = 1 mm.

The two stalks with attached pollen sacs probably served to raise the sporangia above the surface of the subtending scale leaf or allowed them to hang over the edge of the microsporophyll, thus exposing the pollen to wind currents to be carried to the ovules. With no observable nutritive tissue in the microsporophyll or pollen sacs to attract animals, the likelihood of animal involvement in pollination is small. Glossopterid microsporangia are similar to those seen in pteridosperms of the Mesozoic and extant conifers (e.g., *Picea* and *Sequoia*) that rely on wind pollination; these have thin walls and no definite dehiscence point. Studies of anemophily (wind pollination) in angiosperms have noted that species that rely

on this method tend to be located at higher latitudes, are deciduous in nature, produce an abundance of small pollen grains, and have microsporophylls exposed to wind currents (Whitehead 1969). In the Permian, Antarctica was close to or over the South Pole with much of the land mass of Gondwana above 30°S (Wopfner and Casshyap 1997), indicating a seasonal climate for much of the continent. The presence of leaf mats (Plumstead 1958) indicates that *Glossopteris* was a seasonally deciduous plant.

The placement of pollen sacs on the surface of a microsporophyll rather than enclosed in some type of protective structure also supports an anemophilous pollination syndrome. In extant plants, thousands of pollen grains are produced in a microsporangium that is wind pollinated, whereas hundreds of grains are produced in angiosperms that are animal pollinated (Milne et al. 2005). The thousands of pollen grains found in a glossopterid microsporangium (~2656 grains/sporangium; Lindström et al. 1997) supports an anemophilous syndrome. The wide range in size of in situ *Protohaploxypinus* grains (32–176 μm; Lindström et al. 1997) extends beyond the suggested range for wind pollination (20–40 μm) in angiosperms (Whitehead 1969). However, the presence of sacci, each 17–69 μm in diameter (Lindström et al. 1997), in *Protohaploxypinus* adds surface area with a minimal increase in mass, as has been shown to occur in conifer pollen to aid in wind dispersal (Schwendemann et al. 2007). Thus, the majority of the criteria for anemophily are present in the glossopterids, and the potential for wind pollination is well supported.

The Mississippian-Permian Cordaitales have been considered by some authors to be ancestral to the glossopterids (Schopf 1976). A pollen cone of the cordaites (e.g., *Gothania*) is a compound cone of alternating sterile and fertile scales with pollen sacs borne at the tips of the fertile scales (Daghlian and Taylor 1979). Whether all of the scale leaves in *E. macloughlinii* were fertile or whether both fertile and sterile ones were present could not be determined in this study, and White (1978) did not indicate whether the scales in *Squamella* were all fertile or whether sterile scales were also present. In deposits that contain microsporophylls, numerous scale leaves with no sporangial association are found, either isolated in the matrix or present in clusters forming buds (White 1978; Holmes 1995; McLoughlin 2011), which neither supports nor refutes whether glossopterids formed simple or compound pollen cones or even just a fertile region on the plant. In this study, the sporophyll axis is not preserved, and the presence of fertile and sterile leaves in the cone was not observed; thus, it is not possible to determine whether *E. macloughlinii* can be classified as a simple or compound cone. The greatest difference between fertile scales in a cordaite such as *Gothania* and glossopterid microsporophylls is the sporangial attachment; cordaite sporangia are attached to the tip of the sporophylls, whereas the glossopterid sporangia are attached adaxially along the sporophyll.

In addition to the Cordaites, some Paleozoic conifers also show morphological similarities to *Eretmonia*. Pennsylvanian-age walchian conifer microsporangiate structures show some similarities to glossopterid microsporophylls, as they have a prominent distal lamina that is pointed apically, sporangia that can be either sessile or attached to a stalk, and no definitive area of dehiscence (Mapes and Rothwell 1998). Genera of Late Paleozoic–Triassic voltialean conifers—*Dvinostrobus* (Gomankov and Meyen 1986; Meyen 1997), *Darneya* (Grauvogel-Stamm 1978; Kerp 1996), and *Sertostrobus* (Grauvogel-Stamm 1969)—have stalks (sporangiophores) attached on the adaxial side of the scale, much like *Eretmonia*. These cones are considered compound cones, with the sporangiophore produced in the axil or along a subtending sporophyll. If these are considered compound pollen cones, then *E. macloughlinii* may be a compound cone, since the stalks bearing sporangia are adnate to the sporophyll. However, until specimens with more complete preservation are known, defining the cone of *Eretmonia* as simple or compound is premature. While many gymnosperms and pteridosperms have pollen sacs attached to the abaxial surface of the sporophyll/scale, the presence of adaxially attached sporangia is present in the fossil record, supporting the viability of adaxially attached sporangia in *Eretmonia*.

Previous studies (such as Retallack and Dilcher 1981) have suggested that the glossopterids are possible ancestors to the angiosperms on the basis of the morphology of the megasporophylls. In cladistic analyses, most characters for glossopterid microsporophylls have been coded as unknown (Rothwell and Serbet 1994; Doyle 2006; Hilton and Bateman 2006), but with the information provided in this article the mode of dehiscence (ectokinetic) and the position of the pollen sacs in relation to the sporophyll (adaxial) can now be characterized. The helical arrangement of microsporophylls on an axis suggests that the pollen-producing sporophylls of at least one taxon were arranged into a cone. The morphological and anatomical characters of the microsporophylls suggest a phylogenetic position closer to gymnosperms rather than angiosperms.

Conclusions

The description of *Eretmonia macloughlinii* from the Upper Permian of the Transantarctic Mountains provides the first anatomical detail for the microsporophyll genus *Eretmonia*. The helical arrangement of the sporophylls indicates that the microsporophylls of the glossopterids were arranged in a cone. In the glossopterids, the production of pollen sacs on the adaxial surface of the sporophyll is similar to some Paleozoic-Triassic conifers, but it is not common in any other plant group in the Paleozoic or Mesozoic. The distinctive nature of the glossopterids compared with other Paleozoic pteridosperms illustrates that the Permian was a time of transition in the architecture of seed ferns between other Paleozoic forms and those found in Mesozoic strata. The wealth of new data coming from Antarctic specimens collected during the 2010–2011 austral field season illustrates the abundance of information yet to be garnered from Antarctic deposits.

Acknowledgments

We thank the members of the 2010–2011 austral field season central Transantarctic Mountains paleobotany team, including Anne-Laure Decombeix, Ignacio Escapa, Erik Gulbranson, Andrew Schwendemann, Rudolph Serbet, and Brian Staite. We extend a special thanks to the support staff at the

CTAM field camp, as well as additional thanks to two anonymous reviewers for helpful comments that enhanced this article. This research was funded by the National Science Foundation (grant OISE-0825291 to E. L. Taylor and P. E. Ryberg; grant OPP-0943934 to E. L. Taylor and T. N. Taylor).

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